Natural history of thorny devils *Moloch horridus* (Lacertilia: Agamidae) in the Great Victoria Desert

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Abstract

Daily movements and activity of three male and five female thorny devils (*Moloch horridus*) were monitored using biotelemetry in the Great Victoria Desert during September, October and November 1995. Both males and females moved up to 200–300 m daily, with males averaging linear daily distances twice as great as those of females (66.6 m *vs* 31.7 m, respectively). Considerable individual variation in movements is evident among thorny devils. Activity does not appear to be confined to a specific area during the mating season (early spring, August–September). Lizards were considerably more active during early spring (September–early October) than in late spring-early summer (late October–early November). This seasonal activity pattern is reflected in burrow usage which increased significantly during late spring. Males and females were active with similar frequencies. Evidence for *M. horridus* navigating by methods other than sight or smell of another conspecific lizard is presented. Colour correlates positively with activity level ($r_s = 0.45$; $P < 0.0001$), with lighter skin colour associated with higher activity levels. Activity level is correlated with both air temperature and sand temperature ($r_s = 0.263, 0.254$; $P < 0.0035$). Colour is also positively correlated with sand temperature ($r_s = 0.256$; $P < 0.0016$) but not with air temperature. Lizards observed feeding in the morning (before 11 am) were dark in colour and lizards feeding in the afternoon (3 to 6 pm) were light in colour. Foraging behaviour was never observed during about (11 am to 3 pm). Thorny devils undergo rapid weight changes that are not related to oviposition. Fat bodies of females are largest during winter, whereas those of males are largest in summer.

Introduction

Foraging behaviour of lizards is correlated with their morphology, ecology and reproductive characteristics, suggesting an evolutionary relationship among these parameters (Vitt & Congdon 1978; Huey & Pianka 1981; Pietruszka 1986; Perry & Pianka 1997). *Moloch horridus*, the thorny devil, exhibits a bimodal seasonal pattern of activity, with almost no movement during the coldest and hottest months of the year (June and July; January and February) and increased activity during the remaining eight months with mating occurring during spring (Pianka & Pianka 1970). Thorny devils live from six to twenty years (Pianka & Pianka 1970). Additionally, these lizards have a highly specialised diet, consisting almost exclusively of *Iridomyrmex* ants (Pianka & Pianka 1970; Withers & Dickman 1995). Other agamids in the same habitats, for example *Ctenophorus isolepis* and *Ctenophorus inermis*, are more generalised feeders, are active year round, and *C. isolepis* might have a yearly adult turnover (Pianka 1971a,b). Thorny devils are morphologically and ecologically more similar to the North American iguanian *Phrynosoma* than they are to other Australian agamids (Pianka 1994a). *Moloch* and *Phrynosoma* have

undergone convergent evolution and are ecological equivalents (Pianka 1994a, 1997).

Aspects of behaviour and skin colour of *M. horridus* were studied in the Great Victoria Desert during spring to augment our understanding of this unique agamid. Drinking behaviour has previously been documented (Bentley & Blumer 1962; Withers 1993; Sherbrooke 1993). For a century, data have been presented on the number and type of ants consumed daily by *M. horridus* (Saville-Kent 1897; Davey 1923). Little has been reported on the time of day that thorny devils feed in their natural habitat and their corresponding body temperature, or on dynamics of weight gain and loss. Individual thorny devils can vary their colour from light yellow and brown to dark olive gray and brown. Colour changes, which can be rapid, appear to be associated with body temperature, activity level, and camouflage.

We undertook a radiotelemetric study to deduce whether movements of thorny devils were confined to a discernible activity area from mid-September to early November in the Great Victoria Desert (late spring to early summer). Movements were assessed in relation to burrow usage and location. Daily data were collected to identify distance traversed, microhabitats selected, and individual activity level; these were compared with observed skin colouration, time of day and ambient temperature conditions (substrate and air).

Methods

Eight *M. horridus* were located by following their spoor in the sand of the Great Victoria Desert (28° 12' S, 123° 35' E), captured and fitted with external transmitters, each emitting a unique, rhythmic signal (Biotelemetry Tracking, South Australia). Animals were sexed by external appearance (males have a much more bulbous tail base than females). Lizards were measured, weighed, and assigned an alphabetic character for identification.

Between 100 and 200 sets of observations were made during a two month period (mid-September to early November 1995) with 1–2 sets of observations taken each day. Observations were made at different times of day to increase the diversity of activity information. Observers approached the last recorded location of each lizard slowly and quietly, and tried to locate the animal visually before using the audio assistance of the transmitters and a tuned receiver, to minimise interruption of the thorny devil's daily routine. However, in some cases the lizard had clearly noticed the observer before any information on position, activity and/or colour could be recorded.

Each lizard's position was identified at each sighting by triangulation from compass bearings to two of more than a dozen elevated markers. For each position, observations of activity level, colour, nearest foliage, and exposure to the sun were recorded each day. Ambient air temperature and surface sand temperature (in shade or sun, depending on the location of the individual), time of day, and proximity to a burrow were also noted. Ambient temperature was measured daily at 9 am at the Yamarna weather station (Bureau of Meterorology, Perth), located about 8 km northeast of the study site.

Daily positions were plotted for each lizard on an overlay of an aerial photograph of the study site. Points were converted into x and y coordinates for each individual to produce an image of the course and direction of movement. Active and non-active days, total movement, daily linear movement, average daily movement, and maximum daily movement were calculated for two subdivisions of the study period [period A, early spring, 14 September to 20 October; period B, late spring-early summer, 21 October to 8 November] which reflected distinct changes in activity level to further elucidate seasonal changes in movement patterns.

Lizard colour, activity level, temperature, sun/shade exposure and time of day were graded numerically. Activity levels were graded as prostrate (1), upright (2), moving (3), and burrowing (4). Sun exposure was categorised as in full sun (1), in partial sun (2), in shade (3), exposed but cloudy (4) and in burrow (5). Colour descriptions were recorded as dark olive brown (1), olive brown (2), light olive brown (3), yellow (4), or very light yellow (5), although this colour gradient is actually continuous. Temperature and time of day were treated as continuous variables. Data were analyzed using non-parametric Spearman rank correlation coefficients, corrected for ties in temperature or time of day.

In addition to data we collected on these eight individuals, we also report substantial other information collected by ERP over the interval from 1966–1993 at various localities in the western Great Victoria Desert (for dates and localities, see Pianka 1969, 1986, 1994b; Pianka & Pianka 1970); these data include ambient temperature, body temperature, color, and fat body size. For each lizard collected, color was recorded along with body temperature (taken with a thin-bulb Schultheis mercury thermometer) immediately upon capture. Ambient air temperatures were measured at about 1 m above ground. Lizards were dissected in the laboratory and lengths of fat bodies measured to the nearest mm.

Results and Discussion

Dates of capture, weights, snout-vent length (SVL) and sex of lizards monitored are presented in Table 1. Sexual dimorphism is apparent, with females being larger and stouter (Pianka & Pianka 1970). Females averaged 45.5 g ($\pm$ se 5.2) in body mass and 91.0 mm ($\pm$ se 3.6) in SVL. Males were considerably smaller, with an average body mass of 31.2 g ($\pm$ se 1.3) and SVL of 78.7 mm ($\pm$ se 1.8).

Table 1

Identification letter (ID), date of first capture, sex, snout-vent length (SVL), and weights of thorny devils monitored in this study.

ID	Date	Sex	SVL (mm)	Weight at first capture (g)	Weight on 8 Nov, 1995 (g)
M	14 Sept.	♂	82	33.0	(lost 6 Oct)
N	15 Sept.	♀	105	57.0	46.5
O	20 Sept.	♀	88	38.9	49.5
P	27 Sept.	♀	85	28.5	(lost 31 Oct)
Q	27 Sept.	♀	87	52.0	42.5
R	28 Sept.	♂	76	28.5	30.0
S	4 Oct.	♂	78	32.3	(lost 12 Oct)
T	5 Oct.	♀	90	51.0	48.5

Body weight changes

Moloch appear to gain and lose weight quickly. Although we were reluctant to weigh our study animals routinely for fear of disturbing their behaviour, we did document some substantial changes in body mass (Tables 1 and 2). Five lizards were weighed both at capture and at the conclusion of this study (Table 1). The single male (R) gained 1.5 g in 41 days (+5.3 % of initial body mass). Two gravid females (N and Q) lost weight after oviposition and then regained some weight (Table 2) for large overall losses in body mass (-18.4 % and -18.3 % respectively). Another female (O) that did not oviposit gained 10.6 g in 51 days (+27.2 %) (Table 2). Female T did not oviposit but lost 2.5 g in 33 days (-4.9 %). We documented rapid body weight gain following rain by female O. This lizard weighed 40.0 g on 27 September but after a night of rain (on 28 September) it weighed 41.75 g (a one-day weight gain of 1.75 g or +4.4 %, presumably by water absorption). As discussed above, two other females (N and Q) which oviposited on 20 September and 3 October, respectively, were each weighed several times during the course of our study

Table 2

Weights of three female thorny devils on different dates during the study period.

Date	Weight (g)
Female N	
15 Sept	57.0
19 Sept	62.5 (+9.6%)
20 Sept	37.5 (-40.0%)*
8 Nov	46.5 (+24%)
Female O	
20 Sept	38.9
27 Sept	40.0 (+2.8%)
28 Sept	41.75 (+4.4%)
8 Nov	49.5 (+18.6%)
Female Q	
27 Sept	52.0
3 Oct	30.3 (-41.7%)*
8 Nov	42.5 (+40.3%)

* Body weight reductions attributed primarily to observed egg laying

and their body weights fluctuated considerably (Table 2). Each of these gravid females regained considerable body weight rapidly following oviposition (+24 % and +40 %).

Daily and seasonal movements

Average and maximum daily movements for each lizard were calculated (Table 3). Movements were calculated as being linear between successive locations but are therefore underestimates of actual distance moved since lizards usually moved in a non-linear fashion. One male thorny devil (S) was observed for only 8 days before it was lost; it was in or next to its burrow during this time, and therefore it is not included in Table 3. Individual thorny devils differed considerably in the extent of movement; for example, ♂M and ♀N both moved over 1400 m during the study, whereas others moved less than 1000 m.

Table 3

Daily movement parameters of thorny devils divided into two periods; A = Sept 14 to Oct 20; B = Oct 21 to Nov 8. Total distance moved represents a minimal estimate, as indicated in the text. Average daily distance moved is mean ± se.

	Observation period	Total distance moved (m)	Average daily distance moved (m)	Maximum daily distance moved (m)
♂M	A	1436.9	110.5 ± 59.0	310.0
♀N	A	1666.0	47.6 ± 11.0	245.1
♀N	B	44.4	2.5 ± 0.9	12.0
♀O	A	257.3	8.8 ± 2.8	70.3
♀O	B	20.1	1.3 ± 0.5	25.0
♀P	A	312.7	13.6 ± 3.2	59.6
♀P	B	77.5	7.8 ± 3.0	25.1
♀Q	A	827.7	36.0 ± 11.6	177.6
♀Q	B	162.0	9.0 ± 2.0	19.4
♂R	A	1127.9	51.3 ± 10.4	148.0
♂R	B	55.8	2.9 ± 1.1	16.1
♀T	A	294.0	22.6 ± 8.6	102.1
♀T	B	135.6	7.5 ± 2.8	42.8

Table 4

Sexual differences in average daily (mean ± se) and maximum distances travelled by thorny devils observed over the entire period of this study.

Sex	N (days)	Average daily distance moved (m)	Maximum daily distance moved (m)
males	36	66.6 ± 13.3	310.0
females	211	31.7 ± 2.6	245.1

Although movement of individuals varied considerably, data for males and females were compared. Male thorny devils, on average, travelled twice as far in a day as females. Additionally, the longest distance moved in one day by a male (310 m) was 65 m further than the maximum travelled by any female (Table 4). Over the entire period of the study, males moved a greater average daily distance than females ($t_{12} = 3.08$; P = 0.0095 as well as greater maximal daily distances ($t_{12} = 3.48$; P = 0.0046). Males also moved a greater distance than females during the the early spring period (average daily distance, $t_6 = 3.04$, P = 0.0229; maximal daily distance, $t_6 = 4.48$, P = 0.0042), but the sample size was too small for testing significance of differences during late spring-early summer. Comparison of all lizards of both sexes for early vs late seasons also shows a longer movement during the early spring than in late spring ($t_{12} = 3.1$; P = 0.009).

Differences between total days active and inactive for males and females during both periods, compared using contingency table analyses (Table 5), indicate that male activity did not differ from that of females within the two time periods (early and late spring; $\chi^2 = 0.00013$ and 0.00025; P > 0.8). However, a distinct shift in behaviour was noted between time periods. Movements of both sexes were more frequent during early spring than late spring ($\chi^2 = 17.88$, P < 0.0001). Activity changes cannot be attributed to changes in ambient temperature since the difference between average temperatures at 9 am (the only consistent daily temperature measurement made at Yamarna) for the two periods is not significant ($t_{55} = 0.23$). Similarly, average minimum temperatures for each period did not differ significantly ($t_{55} = 0.003$). Inactive days were spent either in shallow burrows or in the shade of a small shrub.

Movements overlain on an aerial photograph of the study area (Fig 1) show that thorny devils. ♂M and ♀N moved over much greater distances than the other thorny

Table 5

Male and female activity (days) given separately for males and females in observation periods A (Sept 14–Oct 20) and B (Oct 20–Nov 8), and combined data for males and females.

	Period A		Period B		Males and Females	
	Male	Female	Male	Female	Period A	Period B
Active	30	84	8	39	114	47
Inactive	13	39	12	52	52	64
% Active	69.8[a]	68.3[a]	40.0[b]	42.9[b]	68.7[a]	42.3[b]

[a,b] frequencies with same superscript do not differ significantly.
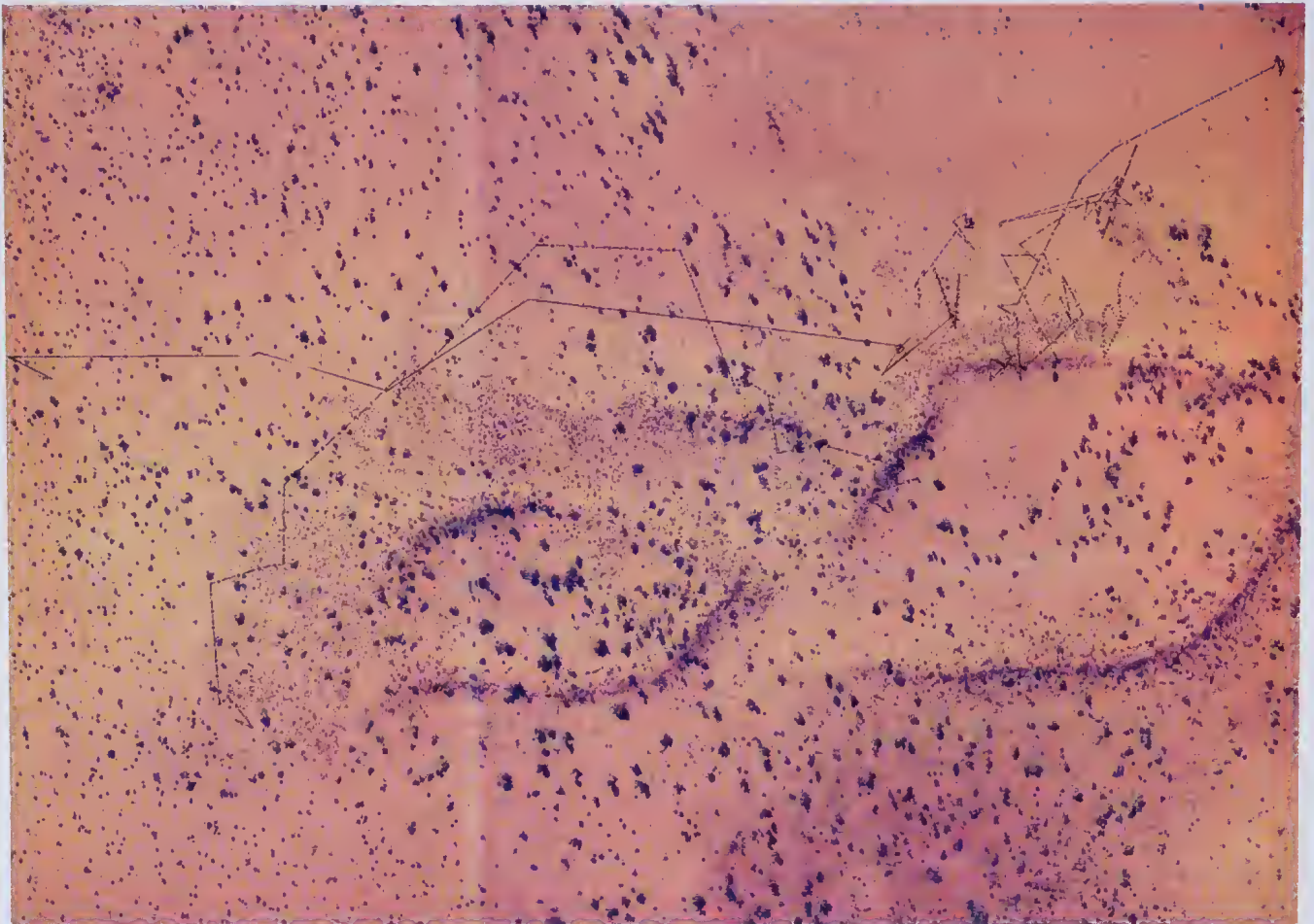
Figure 1. Movements of eight *Moloch horridus* individuals in sandridge habitat of the Great Victoria Desert, between 14 September and 8 November 1995.

devils. No defined activity area was observed for lizards ♂M, ♀N, ♀O, ♂R, or ♀T. Although ♀P repeatedly returned to the same area, its behaviour was anomalous within the context of the study. With more extended study, the relationship between the bimodal seasonal pattern of activity and movements of *M. horridus* might reveal a defined activity area during part of the year.

If the Australian thorny devil has an evolutionary history parallel to its American counterpart, the Texas horned lizard (*Phrynosoma cornutum*), then *M. horridus* might also have shifted away from a strict home range (such as by the agamids *Ctenophorus fordi* and *Ctenophorus isolepis*) towards semi-nomadic behaviour. Guyer (1991) presents two arguments for this shift among *Phrynosoma*, both of which could apply to *M. horridus*. First, the behaviour to freeze rather than run and hide eliminates the need for planned escape routes; and, second, the strict diet of ants might require nomadic movement to follow shifting ant activity patterns (Baharav 1975; Munger 1984). Non-nomadic aspects of behaviour of *M. horridus* might be related to mating rather than evasion of predators (except in the case of gravid females, see discussion on burrow usage) or feeding requirements.

Thorny devils appear to have a navigational ability that cannot be attributed solely to visual recognition or olfactory detection of conspecifics. Although Sporn (1955) described the ability of the thorny devil to perceive flying birds at a long distance, Tollestrup (1983) noted that small lizards are often unable to attain the height necessary to observe others of their species. However, thorny devils might well be able to navigate known terrain by visually locating a specific landmark (*e.g.* a tall shrub). Pianka & Pianka (1970) report finding four thorny devils (two males and two females; individuals of each sex differing in size) at the base of the same large shrub in the early spring on 25 August, 1967 (Fig 2). Such an aggregation of thorny devils had never been previously reported. Winds had erased all tracks the day before. These four thorny devils were back-tracked for varying distances (40–120 m). Two males approached the shrub from the south and south-west at a 90° angle to the path of approach of the larger female, which came in from the east. The smaller female came from the south-west, crossing over the track of the medium-sized male and went to a *Hakea* bush that was also visited by the larger female. Since these lizards converged from 90° compass directions, scents carried by prevailing winds could not have been the primary means by which they navigated. They were also definitely not following tracks of a prospective mate, as we have observed for another local desert lizard, *Varanus tristis* (Thompson *et al.*, in press). We are inclined to interpret this event as a mating rendezvous.

Burrow usage

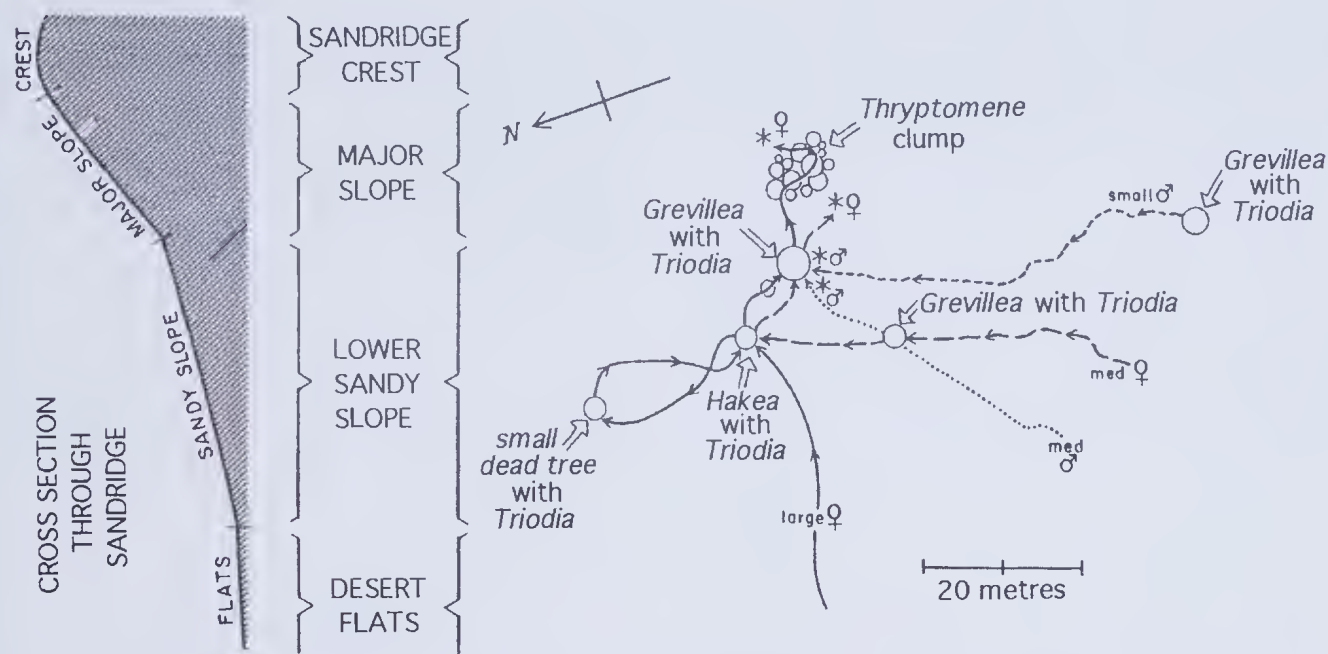Oviposition burrows terminate as an air-filled

Figure 2. Movements of four thorny devils, two males and two females at a study site near Lorna Glen, Western Australia, on 25 August 1967. Strong winds erased all tracks the day before. These four lizards were of different sizes, allowing each individual to be back-tracked for varying distances to establish their movements.

chamber about 8–9 cm high by 10–12 cm wide and about 12–15 cm long, about 20–22 cm below the surface, which is large enough to accommodate several adult thorny devils (Pianka *et al.*, 1996). Non-oviposition burrows are much shallower and smaller than oviposition burrows (only 5–10 cm deep and about 5x5x10–12 cm, just large enough for a single thorny devil). The three male thorny devils (M, R, and S) each frequented only a single burrow during the study period. Females N and Q were gravid at the time of capture and laid their eggs during the observation period. Lizards ♀N and ♀Q occupied non-

oviposition burrows after deposition of their eggs where they remained three to four times longer than they had stayed in their oviposition burrows (Table 6). Oviposition burrows and post-oviposition burrows were at opposite extremes of their observed activity areas. Non-gravid females (♀O, ♀P, and ♀T), although they had no oviposition burrows, also spent more time in their later burrows (Table 6). After mid-October, the single remaining male and four females spent much longer times at the same burrows (Table 6). Pianka & Pianka (1970) suggested that *M. horridus* increases movement (reduces time spent in burrows) in early spring to increase the chance of encounters between prospective mates.

These temporal and spatial patterns suggest that the large scale movements of *M. horridus* might not be random. The 1967 event depicted in Fig 2 occurred in August, just before the calender month in 1995 when multiple gravid females were collected. In 1995, thorny devils were never sighted together and aggregates in this species are rare (Pianka & Pianka 1970; Withers & Dickman 1995). Although *M. horridus* has a life span of six to twenty years (Pianka & Pianka 1970), long term movement data are scarce. Withers & Dickman (1995) report that eight individuals remained within 100 m of the same location after six months and that one had moved 2.5 km after four years. These movements might reflect seasonal mating behaviour, possibly involving long forays to ensure a meeting with other thorny devils and/or a seasonal return to a specific activity area. Since our study period was restricted to late spring, no definitive statements can be made regarding the extent of nomadism present in movements of *M. horridus*.

Thermoregulatory behaviour

Colour is strongly and positively correlated with

Table 6

Burrow use by *M. horridus* (italic entries denote oviposition burrows). Different dates/durations for individuals indicate different burrows are used.

	Date of initial occupation (D/M/Y)	Duration of Occupation (days)
♂M	17/9/95	1
♀N	*16/9/95*	*5*
	24/9/95	3
	16/10/95	2
	25/10/95	14
♀O	20/9/95	2
	16/10/95	16
♀P	11/10/95	1
	16/10/95	3
♀Q	*29/9/95*	*6*
	12/10/95	4
	16/10/95	18
♂R	10/10/95	14
♂S	10/10/95	2
♀T	15/10/95	4
	19/10/95	10
	29/10/95	18

Table 7

Correlation analyses of behavioural response to environment in *M. horridus* (r_s = Spearman rank correlation coefficient corrected for multiple ties; n = number of observations; P = probability of obtaining this level of correlation by chance; NS = not significant).

	r_s	n	P
colour *vs* sand temperature	0.256	153	<0.0016
colour *vs* air temperature	0.139	154	0.0867 (NS)
colour *vs* in sun/shade	-0.110	149	0.1807 (NS)
colour *vs* time of day	0.135	167	0.0839 (NS)
colour *vs* activity level	0.450	136	<0.0001
activity level *vs* sand temp.	0.254	135	<0.0035
activity level *vs* air temperature	0.263	136	<0.0023
activity level *vs* in sun/shade	-0.031	141	0.7161 (NS)
activity level *vs* time of day	-0.120	160	0.1301 (NS)

activity level, indicating that skin colour lightens as activity increases (Table 7). Colour is also positively correlated with sand temperature, with lighter colour at a higher ambient substrate temperature (Table 7). However, colour appears to be independent of sun exposure, air temperature and time of day (Table 7).

The chameleon-like ability of *M. horridus* to change skin colour, thus blending in with surrounding leaf litter, has been known for many years (White 1947; Pianka & Pianka 1970) and was frequently observed during the course of our study, often making it almost impossible to visually locate the transmitting lizards. Data collected by ERP from 1966 to 1992 reveal that although thorny devils can have a high body temperature when dark coloured, they are less likely to be yellow at low body temperatures (Fig 3). The lowest body temperature recorded for a yellow thorny devil was 27.5° C, which is 3.1° C higher
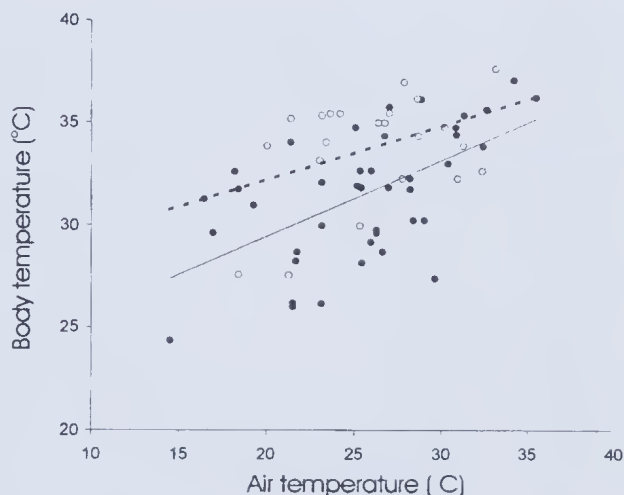
than the lowest recorded body temperature for a dark coloured thorny devil.

Correlations between air temperature and body temperature have previously been reported for thorny devils (Pianka & Pianka 1970, r = 0.625, P<0.01; Withers & Dickman 1995). Individuals were frequently observed flattened against the sand, maximizing contact between body and sand. They were also observed standing on their hind legs, with front legs supported on a shrub. Withers & Dickman (1995) reported that thorny devils can use this posture when eating ants; we also observed thorny devils in this position when no ants were visible. Based on these observations and the correlation between air and body temperature, *M. horridus* does not appear to be a passive thermoconformer, but basks (is heliothermic) and may use contact with the sand (is thigmothermic) to regulate its body temperature.

Foraging behaviour

Thorny devils are classic "sit-and-wait" predators (Pianka 1966; Perry & Pianka 1997), although they probably select their feeding sites with care. Thorny devils were observed feeding only during the morning before 11 am and afternoon between 3 and 6 pm. In the morning, all twenty foraging individuals were various shades of olive/brown. In late afternoon, the three foraging thorny devils were light yellow. Of 46 observations on thorny devils made between 11am and 3pm, none were feeding. Consumption of ants was recorded only when animals were near a *Triodia* tussock or *Thryptomene* shrub and when sand temperatures were at least 24° C and occasionally above 40° C. Ants might be consumed independently of body temperature with use of camouflage darkening tactics complicating our observations.

Fat stores

Like many lizards, *Moloch horridus* stores lipids in paired fat bodies that protrude into the postero-ventral body cavity. Fat body lengths for a large series of thorny devils collected at various times of the year (measured by ERP) show that fat body cycles differ for males and females. Female thorny devils have a seasonal variation in fat body sizes, with smaller fat bodies during summer and larger fat bodies in winter (Fig 4, lower panel), but no such trend is evident among male thorny devils (Fig 4, upper panel). This sex-specific difference is probably a direct consequence of oviposition by females. To produce a clutch of eggs in the early spring, females must mobilize their fat reserves, which are then replenished during autumn.

Figure 3. Relationship between body temperature and ambient air temperature for *Moloch horridus* with light (open symbols) and dark (closed symbols) body colour. Least squares regression line for light-coloured lizards is significantly higher than for dark-coloured lizards (ANCOVA; $F_{1,62}$ = 16.6, P < 0.0001; slope t_{62} = 0.71, P > 0.50, NS; elevation t_{63} = 7.45, P< 0.001). Regression equations relating body temperature to ambient air temperature (T_a; °C) are for dark colour (——; T_b = 21.89 + 0.371 T_a; r^2 = 0.34) and for light colour (— — —; T_b = 26.97 + 0.261 T_a; r^2 = 0.16).

Conclusions

This study emphasises the usefulness of colour in indicating behaviour patterns of thorny devils. The colour of a thorny devil colour reflects its activity level unless the lizard has darkened its skin and crouched in the leaf litter or shade, presumably to elude a potential predator. These lizards appear to be both heliothermic (sun bask) and thigmothermic (adjust their body contact with the sand) to regulate their body temperature. Further and more detailed studies with
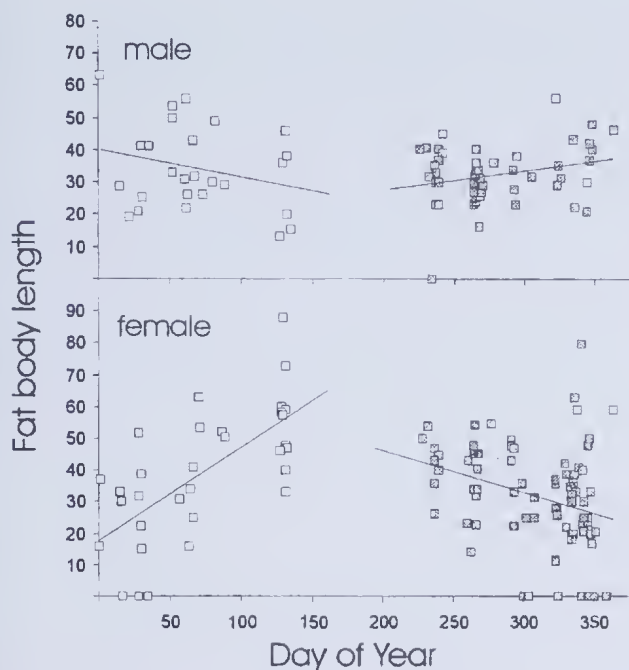
Figure 4. Annual cycle of fat body lengths for male (top) and female (bottom) thorny devils (1 = Jan 1 and 365 = Dec 31). Raw data (the sum of lengths of both fat bodies for each lizard) are plotted for each lizard (two data points are coincident for a few values). Least squares linear regressions fitted to data for the first half and second half of the year are also shown. Slopes for males and females are opposite in sign and significantly different (tests of parallelism; first half year, $F_{1,56}$ = 18.58, P < 0.000067; second half year, $F_{1,130}$ = 9.93, P < 0.002). Regression equations (coefficients significantly different from zero are shown in boldface type); early males, y = 39.84 − 0.084x (r^2 = 0.027; P = 0.2002); early females, y = 17.475 + 0.298x (r^2 = 0.452; P < 0.0001); late males, y = 11.494 + 0.072x (r^2 = 0.069; P = 0.0317); late females, y = 70.78 − 0.125x (r^2 = 0.071; P = 0.0093).

multiple daily body temperature measurements of individual lizards in a natural environment are needed to confirm this suggestion.

Thorny devils were never observed to feed in mid-day during spring. The majority of thorny devils that were observed to forage were feeding in the morning and were a dark color (indicative of either a low body temperature or active camouflage). Feeding could be independent of body temperature, but further studies of natural foraging behaviour and concommitant body temperature are needed to clarify this relationship.

In a natural environment, thorny devils can gain and lose weight rapidly. Large weight changes accompany oviposition as noted previously (Pianka *et al.* 1996), but here we report substantial, non-ovipositional weight changes over variable time periods. Fat body cycles differ between the sexes, probably because females must invest lipids in egg production during early spring. Additional field work is needed to (1) record rates of weight gain and loss, (2) measure the percentage of weight gain due to water absorption and/or ant consumption, and (3) to interpret the functional significance of these rapid changes in body weight.

Thorny devils can travel long distances (up to 200–300 m per day) and undertake such movements in early spring. Seasonal fluctuations in burrow use and daily

movements reflect the bimodal annual pattern of activity reported by Pianka & Pianka (1970), further indicating the uniqueness of this agamid. Increased movements may be a part of seasonal mating behaviour governed by visual detection of large landmarks such as shrubs. Patterns of burrow use suggest that gravid female *M. horridus* might travel to a spot away from their non-oviposition burrows to deposit their eggs. Further movement studies are necessary to ascertain whether this species is entirely nomadic, semi-nomadic or maintains a home range. Seasonal data on male and female movements from immediately prior to our study period (August to mid-September) would clarify whether non-oviposition burrows were occupied before egg deposition, which could indicate that they are part of an annually occupied area.

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